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Interspecific Competition and the History of *Pieris rapae* in North America

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Workers on a particular group of organisms often engage in discussions of quite general phenomena while maintaining a rigid parochialism. The recent discussion of interspecific competition in butterflies between Messrs. Sevastopoulo (1973), *Ent. Rec.*, 85: 247) and Luckens (1974, *Ent. Rec.*, 86: 71-72) is a case in point; although Luckens refers to competition as a recognised concept "in all fields of zoology", both by and large act as though butterflies were likely to be unique among living things in their competitive relationships (or lack of them). Yet interspecific competition has engaged the attention of both field and theoretical ecologists and has been studied in vertebrates, invertebrates, plants and microorganisms, and the literature of the subject is immense! A commonly held view among American ecologists is that interspecific competition is a very important organising force in biotic communities, acting on at least two levels: firstly, in cases where niche overlap is initially very great, by direct exclusion in ecological time; secondly, promoting divergence of the niches of partial competitors through natural selection in evolutionary time. Opponents of the concept of interspecific competition often point to the seeming rarity of documented instances in nature; its supporters observe that by their view episodes of competition are transient, leading to exclusion or ecological divergence, so that in most cases organisms in stable communities will already have divided up their resources before we ever get a look at them.

The most important instances for the study of processes operating in competition occur when species are introduced, as on a new continent, and their interactions with the pre-existing biota may be observed. An excellently documented case concerns the deliberately introduced entomophagous Hymenoptera of the genus *Aphytis* (DeBach and Sundby, 1963, *Hilgardia*, **34**: 105/166). Even here the actual mechanism of exclusion is not understood, if the fact of exclusion is undeniable. Unhappily, many much less well-documented examples have gained unwarranted currency in the literature, and one of these is the case of *Pieris* in North America, cited by Luckens.

I do not propose to trace the history of this reputed interaction in the literature in this note, but very briefly the facts are these: *Pieris rapae* L. arrived in North America uninvited about 1860 and in the next several decades various authors recorded the decline and disappearance of the native species, *P. napi* L. and *P. protodice* Boisduval and LeConte, which many of them were inclined to attribute to the arrival of the immigrant. It seems clear that *napi* did disappear at least in parts of southern New England and western New York. It is equally clear that where the forest cover remained virtually intact, *napi* showed no such diminution even in the north-eastern states, nor anywhere in the west. Hovanitz (1962, *J. Res. Lepid.*, **1**: 77) argues quite plausibly that the decline of *napi* was occasioned by removal of the forest with advancing agriculture and urbanisation. However, we do have to account for the known presence of *napi* in such places as Harvard Yard, which had been in an unnatural state for very many years, and from which *napi* disappeared supposedly with the advent of *rapae*. I do not see any difficulty with this. In much of its Holarctic range *P. napi* occurs in open as well as forested habitats—in Britain it, not *rapae*, is found in sedgy swales, for example. In the absence of any competitor it undoubtedly moved out of the still-nearby forests into agricultural and urban New England, and was able to thrive until *rapae*, which was preadapted to such habitats, displaced it from them. *Napi* today is probably restricted to the habitats it held in the north east before the white man came—habitats now much reduced in area; those from it was ultimately ousted were man's doing in the first place, and *napi* was, for a few decades, a beneficiary of civilisation before it became its casualty.

Pieris protodice is quite another matter; I have been unable to find grounds to accept that it has been restricted either ecologically or geographically by *rapae*. *Protodice* is a *Pontia*, with the usual preferences of that subgenus; ecologically it is very nearly the equivalent of the European *daplidice* L. In the summer-arid and semi-arid parts of North America it is everywhere the most abundant *Pieris*, at least below 1,500-2,000m, yielding to *rapae* only where agricultural irrigation is widespread or winters are cold or very humid or both. In the north east it is virtually restricted to the sunniest, driest, hottest places:

in fact it is today very abundant in railway switch-yards, urban vacant lots, and the like — places where Lepidopterists seldom go, so *protodice* does not appear on their lists. I have seen it flying by thousands in the very places where William Beutenmuller saw it in New Jersey 75 years before; yet F. M. Brown's New Jersey correspondents assured him it is virtually extinct in that state (Brown, 1973, *Trans. Amer. Ent. Soc.*, **99**: 107)! That it is climatically restricted is graphically demonstrated by its consistent inability to overwinter on the Piedmont a few kilometres north and west of Philadelphia, although it does so regularly on the Atlantic Coastal Plain within and south-east of the city. Similarly, it occurs abundantly about New York City in the boroughs of Queens and Kings (Brooklyn), which are on Long Island, and on Staten Island, but not on the adjacent mainland.

In Europe *Pieris rapae* occupies an ecological position intermediate between *P. napi* on one hand and *P. daplidice* on the other. In North America, where no corresponding species occurred, it has fit itself in between *napi* and *protodice* in similar fashion. In the absence of careful historical documentation it would be quite impossible to discriminate between the situation on the Continent, where the three species have presumably coevolved over a very long time, and in the U.S.A. where they have not. As usually happens the historical opportunity was largely missed, and the case requires a somewhat more cautious interpretation than that of Klots. This is all the more important since it has now gained entry to the British literature and could become proverbial there even as its significance is being revaluated at home; at any rate the reality or unreality of competition (even in one taxonomic group) should not ride on the fate of any particular example!

To return to more general matters, the argument that herbivores cannot be in competition because they do not defoliate plants was at the heart of a noteworthy exchange in the ecological journals several years ago (Hairston, Smith, Slobodkin, 1960, *Amer. Naturalist*, **94**: 421-425; Murdoch, 1966, *Ibid.*, **100**: 219-226; Ehrlich and Birch, 1967, *Ibid.*, **101**: 97-101). In this exchange it was pointed out that, for biochemical or other reasons, the amount of foliage we observe is not necessarily the same as the amount "available" to an animal. In a recent study (now in press) I examined temporarily sympatric populations of *Pieris protodice* and *P. occidentalis* Reakirt feeding on the same species of pepper-grass (*Lepidium*). Although the overall impact of both species on the plant population was minute, oviposition was very clearly non-random, with females of both species preferring isolated plants and those at the edges of dense stands, and these were commonly defoliated although the plants within the stands were untouched. I am certainly not willing to say there were "Cruciferae enough for all"!